ROCK-DESTROYING ORGANISMS IN RELATION TO CORAL REEFS

BY

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WITH SIX PLATES AND FIVE TEXT-FIGURES.

CONTENTS

I. INTRODUCTION

Under tropical conditions rock-boring organisms attain an enormous variety both in numbers of genera and species, and it would be expected that they play an important part in the economy of coral reefs. Considering the undoubted importance of these organisms in the biology of any coral reef when taken as a whole, it is surprising how few of the numerous workers engaged in this subject have mentioned them. Nevertheless, many of these organisms have provided most interesting biological studies as individuals, but it was left almost entirely to Gardiner (1903*a*) to raise the question of the importance of these organisms in coral reef destruction. No general account corresponding to that of Calman (1936) has yet been written about these tropical species. A proper understanding of the relationships between those organisms that build and help to protect reefs, and those that aid, directly or indirectly, in their destruction is essential to the proper understanding of the whole. A coral reef consisting geologically of a comparatively soft limestone rock is, as would be expected, an ideal home for rock-burrowers utilizing both mechanical and chemical methods, but their destructive effects are not always apparent. The reason for this masking of their action lies in the state of the reef. According to certain recent theories there exist, perhaps nowhere in the world at the present day, coral reefs that are appreciably growing, *i. e.* increasing in area against the various factors of destruction, but there are many that are actually holding their own, while there are also large areas in the process of destruction, as well as many dead and dying reefs in various stages of decomposition, regions in a single reef often exhibiting all these stages. In a reef, or area of a reef, rich in living coral, as well as in those animals and plants which form protecting surfaces, the effects of boring organisms are masked and consequently inconspicuous, and play a small part in the economy of the reef as a whole. On the other hand, in those reefs in which the factors of erosion have attained the upper hand, boring organisms may become more conspicuous.

Almost all the observations on these organisms and most of the collections that were formed were made at Low Isles, for a full geographical and geological description of which see Stephenson, T. A. & A., Tandy and Spender ('G.B.R. Exped. Reports', Vol. III, No. 2, and Spender, 1930). Small collections were also made at Batt Reef on the outer barrier. The rock-burrowing fauna at Low Isles probably represents a high percentage of that found on neighbouring areas of the Barrier Reef, although many of the Molluscan borers do not attain so large a size. The island, being within seven miles of the mainland, is within the range of the flood waters of some of the rivers, the silt and the lowering of salinity at these times possibly affecting the boring fauna, although to a lesser degree than animals in other habitats. All the types of coral limestone at Low Isles are, however, vigorously attacked by borers in favourable localities. Investigations were carried out between tide-marks and, where possible, to a few feet below low water of spring tides. The rock-burrowing Mollusca received by far the greatest attention.

I wish to take this opportunity of thanking Prof. Stanley Gardiner, F.R.S., and Prof. C. M. Yonge for the valuable assistance they have given me both while the work was in progress and during the writing of this paper, and to Dr. W. T. Calman, F.R.S., and Mr. Robson, of the British Museum (Natural History), for many kind suggestions.

II. SYSTEMATIC CLASSIFICATION OF THE ORGANISMS WHICH DESTROY CORAL ROCK AT LOW ISLES

The rock-destroying organisms occurring at Low Isles can be classified as follows :

I. ANIMALS.

A. SPECIALIZED ROCK-BURROWERS.

The animals included under this heading are so specialized for this habit as to be unable to live otherwise than in a burrow. The majority, if removed from their burrows, are unable to make fresh ones. Many of the burrows are deep and complex in structure and completely conceal the animal from view. The following occur at Low Isles :

MOLLUSCA. Lamellibranchia.

Lithophaga cumingiana (Reeve).
L. obesa (Philippi).
L. hanleyana (Reeve).
L. teres (Philippi).
L. argentea (Reeve).
Modiolus cinnamomeus (Bruguière).
Gastrochaena laevigata Deshayes.
G. cuneiformis Spengler.
Petricola lapicida (Gmelin).
Tridacna crocea Lamarck.
T. maxima (Röding), var. *fossor* Hedley.
Arca imbricata Bruguière.

The species of the genera *Lithophaga*, *Modiolus*, *Gastrochaena* and *Petricola* were kindly identified for me by Mr. J. R. le B. Tomlin at the British Museum. The list of Mollusca given in the ecological reports of the expedition (Stephenson and others 'G.B.R. Exped. Reports', Vol. III, No. 2, p. 59 and 110) differs in the naming of *Lithophaga hanleyana* and *Gastrochaena cuneiformis*, which are presumably given as *Lithophaga subula* and *Gastrochaena gigantea* respectively. *L. subula* does not occur at Low Isles, while *L. hanleyana* does. On comparing the specimens of *Gastrochaena* from Low Isles with those in the collections of the British Museum, Mr. Tomlin and the author have come to the conclusion that *G. laevigata*, *G. cuneiformis* and *G. gigantea* are probably one and the same species.

CRUSTACEA. Cirripedia.

Lithotrya valentiana (Gray).

Only one species of rock-burrowing barnacle was found at Low Isles, the morphology of which is described by Cannon ('G.B.R. Exped. Reports', Vol. V, No. 1).

GEPHYREA. Sipunculoidea.

Aspidosiphon steenstrupii Diesing.
Physcosoma scolops (Selenka and de Man).
Cleosiphon aspergillum (Quatrefages).

The three species mentioned above are the only (presumably) rock-burrowing forms identified from the expedition's collections (Monro, 'G.B.R. Exped. Reports', Vol. IV, No. 1, pp. 34–35), although others probably occurred.

POLYCHAETA.

True rock-burrowing species undoubtedly occurred, but were not collected. Several species identified by Monro ('G.B.R. Exped. Reports', Vol. IV, No. 1) from the expedition's collections were labelled "from rocks", but there is no information to determine whether these were true rock-borers or species that had crawled into old Polychaete or Sipunculid burrows.

PORIFERA. Tetraxonida.

Spirastrella inconstans (Dendy).
S. aurivillii Lindgren.

These were the only two boring sponges identified by Burton ('G.B.R. Exped. Reports', Vol. IV, No. 14, pp. 570–571), from the expedition's collections. Others most probably occurred, and some of the mature forms identified may be rock-borers in their early stages.

B. ANIMALS WHICH FORM BURROWS OR SHALLOW CAVITIES ON ROCK SURFACES FOR A PROTECTION DURING PERIODS OF UNFAVOURABLE CONDITIONS.

These animals, if removed from their burrows, are usually able to exist without them or can make fresh ones when necessary. The burrows may vary in depth from shallow cavities to deep pits, and are either made by the animal itself, or were previously in existence and enlarged by the animal. The following occur at Low Isles:

ECHINODERMATA. Echinoidea.

Echinometra mathaei (de Blainville).
Echinostrephus molare (de Blainville).

These were identified by Clark ('G.B.R. Exped. Reports', Vol. IV, No. 7, pp. 215, 216) from the expedition's collections.

MOLLUSCA. Amphineura.

Acanthozostera gemmata (de Blainville).

Other burrowing species probably occurred.

C. ANIMALS WHICH RASP ROCK SURFACES WHILE FEEDING.

Several of these animals also form slight cavities for themselves on the rock surface. Under this heading can be placed the various Echinoids, Amphineura and Gastropod Mollusca (*Nerita*, etc.), which possess this feeding habit, as well as, probably, certain fish.

D. ANIMALS WHICH FEED DIRECTLY ON LIVING CORAL.

Some of these animals bite away portions of the calcareous skeleton together with its surface layer of polyps. According to Stephenson, and others (' G.B.R. Exped. Reports ', Vol. III, No. 2), living coral was not observed to be attacked at Low Isles, but there are certain fish (*e. g. Pseudoscarus*), some Gastropods and other carnivorous animals which are known to eat living coral polyps in other localities.

II. PLANTS.

Certain algae (Chlorophyceae, Cyanophyceae and Rhodophyceae) and fungi (or perhaps saprophytic algae) have been recognized as burrowing in or making surface impressions upon corals, mollusc shells and calcareous rocks (Bornet and Flahault, 1889 ; Duerden, 1902 ; Duncan, 1876 ; Johnson, 1894) from quite early times. Although no collections were made of these most important rock-destroying organisms, some of them undoubtedly occurred at Low Isles as they do upon all reefs.

III. THE MODE OF LIFE OF ROCK-BURROWING ORGANISMS

The organisms using mechanical methods of boring include, among the Mollusca, species of the genera *Petricola*, *Gastrochaena*, *Tridacna* and *Arca* (as well as all those Gastropods and Amphineura, such as *Acanthozostera*, which in feeding rasp away the outermost surface of the rock), the barnacle *Lithotrya*, the majority of the Polychaeta, possibly some of the Porifera, the Gephyrea and the Echinoids.

The mechanical method of rock-burrowing, owing to the necessity for removing a substance as hard or harder than anything in the animal's body, often leads to peculiar morphological specializations being developed among many of the groups concerned. In the Lamellibranch Mollusca :

(1) Distinct abrasive outgrowths may be developed on the outside of the shell (*e. g. Pholas, Gastrochaena*, etc.).

(2) The ligament and hinge may degenerate, thus enabling the valves to move independently in different planes (*e. g. Pholas*, etc.).

(3) Certain foot muscles may become so greatly developed as to render possible a partial rotation of the shell within the burrow (*e. g. Pholas*, *Gastrochaena*, *Saxicava*).

(4) The byssus may be greatly developed (*e. g. Tridacna* and *Arca*).

In the Pedunculate barnacle *Lithotrya*, the peduncle is studded with minute calcareous projections, while the rock-burrowing Sipunculids are armed, often at both their anterior and posterior ends, with discs of hard chitinous teeth. In many of the rock-burrowing Polychaeta the jaws are strongly developed (*e. g. Eunice siciliensis*), while others are said to bore by means of the setae on the parapodia. The Echinoids use both their spines and teeth.

Under a second heading may be placed the species of Lamellibranch Mollusca of the genera *Lithophaga* and (probably) *Modiolus*, the Algae, and possibly some of the Polychaeta and Porifera, which seem to bore by chemical means. Calcareous rocks only are inhabited, the rock being dissolved away by an acid secretion. No definite acid has been identified, and many rock-burrowing animals are placed under this heading on no other evidence than restriction to calcareous rocks, and the absence of any of the specializations characteristic of mechanical borers. Hydrochloric acid seems most likely to be employed by these animals, although an organic acid, or mixture of acids, may conceivably be used. Carbonic acid, produced in respiration, is considered to be utilized by most of the boring algae (Duerden, 1902), and is stated by Carazzi (1892) to be used by *Lithophaga*. In all cases the rock is removed in solution. Immediate neutralization on contact with the surrounding rock together with the minuteness of the quantity secreted at any one time add to the difficulties of detecting the free acid.

A. THE METHOD OF BORING AND DESCRIPTION OF THE BURROWS.

(i) MECHANICAL BORERS.

1. Mollusca. Lamellibranchia.

Petricola lapicida. (Plate I, fig. 1[1].)

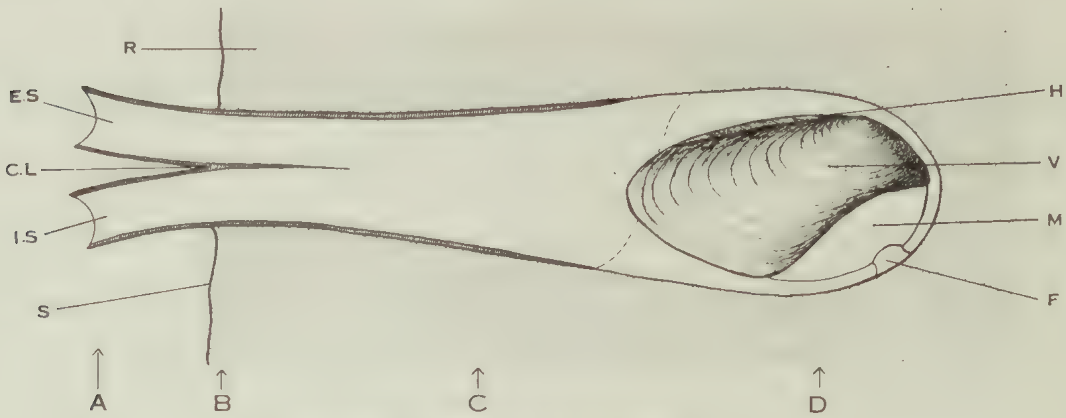
The shell of *Petricola lapicida* (Plate I, fig. 1[1]) appears less adapted than others of this genus for rock-burrowing. In shape it is very similar to many sand-burrowing Lamellibranchs, but in addition is particularly thick, with external serrations. These serrations are well developed posteriorly, where they run longitudinally, their terminations forming a jagged posterior margin to the valves. Around the umbo and on the anterior and ventral surfaces the serrations are very minute, but sufficient to give the shell a rough appearance. The thickness of the shell and its serrations are the only characters that can be considered specializations for mechanical boring. The siphons are long and are separated from each other for their whole length, and extend for a considerable distance above the surface of the rock and so clear of any surrounding growth. Their ends are pigmented and may be light-sensitive. The siphons do not lay down calcareous linings around themselves. The burrow is shallow, very little deeper than the length of the shell, and oval in transverse section. The entrance to the burrow is roughly oval in shape, the posterior margins of the valves being only just below the surface, and on the rock surface appears to consist of two separate holes, the apertures of the inhalent and exhalent siphons. These two apertures are not in the substance of the rock, however, but only pass through algae growing around the entrance, or detritus kept in place by mucus secreted by the siphons. Boring is presumably mechanical, the animal working its way into the rock when enlarging the burrow during growth. The opening and shutting of the valves and the consequent friction of their surfaces against the walls of the burrow would be sufficient to enlarge this as growth proceeded. Leverage applied by the foot would undoubtedly help the valves in their grinding action, but from the oval shape of the burrow and its comparatively close fit, it does not appear that any rocking or rotating movement is employed as in the more specialized mechanical borers. Enlargement of the posterior region of the burrow, and the entrance, in order to allow for the increase in diameter of the siphons, probably takes place by the rasping action of the posterior ends of the valves.

Arca imbricata.

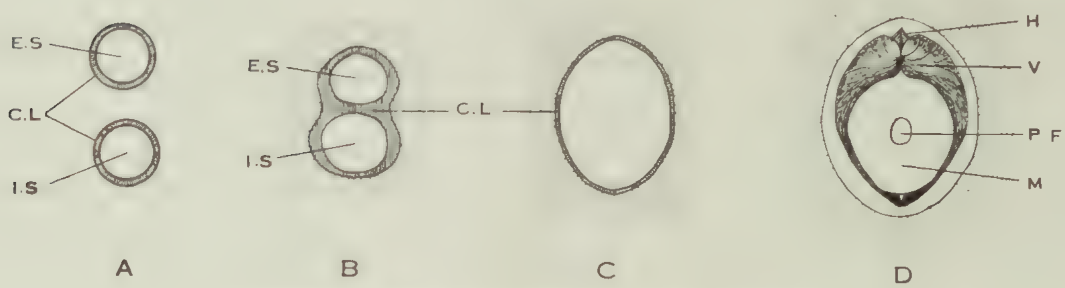
The impressions made by this species upon rocks can hardly be described as burrows, for they are shallow and inconspicuous and the animal is not hidden from view. This lamellibranch is attached to the rock surface along its ventral side by a powerful byssus, which emerges from the shell through a large pedal opening between the valves at about the middle of the ventral margins. The burrows appear to be excavated by the ventral regions and margins of the valves on opening and closing, and on being pulled in towards the rock by the byssus, the presence of the pedal opening prevents the byssus from being undercut by the edges of the valves.

Gastrochaena laevigata and *Gastrochaena cuneiformis*. (Plate I, fig. 1[2, 3]; and Plates I, fig. 2 and II, fig. 1.)

The two species of *Gastrochaena* occurring at Low Isles, *G. laevigata* and *G. cuneiformis*, only differ from each other as regards the shape of the shell, the former (Plate I, fig. 1[3], species having more rounded posterior margins to the valves than the latte (Plate I, fig. 1[2]). Their burrows are, however, very similar. The shell (Plate I, fig. 2) is thin, gapes widely anteriorly and has no periostracum. The surface is slightly rough. The mantle is fused ventrally along its whole length, except for a small pedal orifice anteriorly, through which protrudes the foot (Plate I, fig. 2). This orifice is capable of being opened and closed by muscles in the mantle walls, and the foot can be completely retracted within the mantle cavity. The foot is very powerful, and when protruded can anchor the shell firmly against the anterior region of the burrow by suction ; there is no byssus. The siphons are long and are united along their whole length, except for a short distance before their extremities. The ends of both siphons are coloured brown, and as in *Petricola lapicida*, *Pholas dactylus* (Lindsay, 1912) and *Lithophaga lithophaga* (List, 1902), are apparently sensitive to light. The siphons secrete a calcareous lining around themselves as in *Teredo* and *Lithophaga*, and as in *Teredo* this calcareous lining is uniform in thickness around both siphons. The entrance to the burrow (Text-fig. 1) is very characteristic, being through two circular apertures of approximately the same diameter, the holes being separated from each other by a very thin calcareous partition (Plate II, fig. 1). This partition separating the circular apertures of the inhalent and exhalent siphons extends only a short distance downwards (anteriorly), corresponding to the distance that the two siphon extremities are separated from each other. In some cases the external apertures of the siphons are carried above the rock surface in order to clear surrounding algal growth, their calcareous linings forming a tube, which in one case projected $1\frac{1}{2}$ in. above the surface. Analogous conditions were found by Yonge (1927) in the case of *Teredo norvegica*. Pieces of wood in which the burrows occurred happened to be so placed in an aquarium tank that the faeces from the animal were deposited around the siphon apertures. At the end of four months the surrounding faecal deposit was removed, when it was found that the siphons had prolonged their calcareous tubes through the deposit. A transverse section (Text-fig. 1) of the siphonal region of the burrow made some distance from the entrance is hour-glass shaped, with only a small calcareous outgrowth from the sides forming a constriction between the siphons. The burrow has this shape of section anteriorly as far as the region occupied by the shell, which is globular, almost circular in transverse section and bare of any calcareous lining (Text-fig. 1). In *G. laevigata* the transition from the siphonal region to that region occupied by the shell is very sudden, the burrow passing from a dumb-bell-shaped section to an oval section with very little previous expansion. In *G. cuneiformis*, on account of the more pointed posterior ends of the valves, the transition is more gradual. If the calcareous lining secreted by the siphons is removed, the burrow is found to be in the form of a very elongated cone with a rounded base and oval in transverse section. This gives the impression, independent of any modification of the shell, that boring is mechanical, and that the calcareous lining to the burrow secreted by the siphons is purely superficial on a region of the burrow originally carved out by the passage of the growing shell. The morphology of the animal strongly suggests mechanical boring of a type similar to, but not so specialized as, that of *Pholas* or



Longitudinal section of burrow.



Transverse sections of burrow at A, B, C and D.

TEXT-FIG. 1.—Burrow of *Gastrochaena cuneiformis* in section. (× $1\frac{1}{2}$.) CL, calcareous lining; ES, exhalent siphon; F, foot; H, hinge; IS, inhalent siphon; M, mantle; P, pedal opening; R, coral rock (coarsely stippled); S, surface of the rock; V, valves of the shell. The dotted line shows the anterior limit of the calcareous lining to the burrow.

Teredo. From the oval section of the burrow, it appears that a rocking movement of the shell comparable to that of *Pholas* may occur. This would be possible owing to the powerful pivoting action of the suctorial foot, the anterior areas and edges of the valves grinding away the rock. Boring might also be aided by the opening and shutting of the valves, which would bring the anterior surfaces of the shell into frictional contact with the walls of the burrow. Suction, caused by the lips of the mantle around the pedal orifice, as described in aiding the burrowing of *Saxicava rugosa* and *Pholas dactylus* by Elliott and Lindsay (1911) and by Lindsay (1912), may also occur. The suctorial foot can be planted in other positions so that different areas of the burrow can be brought under the action of the valves. The shell is indeed thin, but, as in many species of *Pholas*, hard although fragile. The anterior edges of the valves can be rapidly renewed by the pallial margins. This region does not show the effects of wear as much as the regions around the umbones, which in many specimens appear particularly thin. Compensation for wear in this region takes place by the thickening of the shell on the inner surface. The increase in diameter towards the mouth of the burrow with the growth of the siphons is, however, more difficult to explain, the siphons apparently possessing no mechanical device for enlarging the diameter of their tubes. The difference between an old and a young individual in the diameter of the siphons at their extremities is small in comparison with that at their base, but such growth as does take place near the mouth of the burrow can only be accommodated by the removal of the rock before the calcareous lining is laid down. It is possible that this lining may be periodically dissolved and laid down afresh. In several molluscs the action of secreting calcium carbonate has been proved to be to some extent reversible, and it seems likely that the external tissues of the siphons of *Gastrochaena* may possess this dual power, and at times dissolve away portions of their own calcareous lining, and perhaps the rock substance itself around their apertures.

Tridacna crocea and *Tridacna maxima*, var. *fossor*.

The method of boring, form of the burrows and the ecology of the above two species are fully described by Yonge ('G.B.R. Exped. Reports', Vol. I, No. 11), and will be only briefly summarized here. Boring is purely mechanical. The young individual does not begin to burrow until approximately 1·5 cm. long, but remains attached in a hollow on the surface of the rock by means of its byssus. On account of the peculiar twisting round of the mantle and shell in *Tridacna*, the pedal opening and byssus come to lie just posterior to the hinge, so that the animal burrows hinge foremost. Burrowing begins by longitudinal and lateral rocking of the shell when the animal is pulled down against the surface of the rock by the byssus, the grinding-away of the rock taking place by means of the ridges on the surface of the shell. As burrowing and growth proceed, the shell enters obliquely, ventro-anteriorly, into the surface of the rock, and the pedal opening and byssus move more posteriorly; thus the area of attachment is not undercut, except anteriorly, but remains as a projecting pillar within the burrow. The animal eventually becomes imprisoned within its burrow. Of the two species *T. crocea* (Yonge, 'G.B.R. Exped. Reports', Vol. I, No. 11, Plates II, III and IV; and Stephenson and others, 'G.B.R. Exped. Reports,' Vol. III, No. 2, Plate VI, figs. 3 and 4) is the more specialized, *T. maxima* var. *fossor* (Stephenson and others, 'G.B.R. Exped. Reports', Vol. III, No. 2, Plate XVIII, figs. 3 and 4) usually occurring in coral fragments which have been cemented together. *T. maxima* var. *fossor* is called *T. fossor* by Stephenson and Yonge in their papers.

2. Mollusca. Amphineura.

Acanthozostera gemmata.

Acanthozostera gemmata (Stephenson and others, 'G.B.R. Exped. Reports', Vol. III, No. 2, Plate XXI, fig. 2) is the commonest "Chiton" at Low Isles which forms hollows for itself, but possibly other burrowing species occur. These hollows are shallow, resembling those made by certain Echinoids and Gastropods (*e. g. Patella*), and the animal is able to emerge at times to feed. At low tide, and during storms, the animal can anchor itself so firmly to its hollow by means of the foot that dislodgment is often impossible without injury. Like certain burrowing Echinoids the animals normally return to the same burrow or one that fits them, but sometimes they are compelled to distort themselves in order to enter crevices and old *Lithophaga*-burrows, which are later enlarged to the required shape and size. From the nature of the internal surface of the hollow it appears that the radula is used for excavating, perhaps aided to a slight extent by the calcareous tubercles on the mantle when the animal settles within its burrow. Small heaps of faeces are often found around the animals when in their hollows. These are calcareous, being soluble in dilute acid, and are composed of rock that has been rasped off along with superficial algae when feeding, as well as that which is removed when enlarging a hollow.

3. Polychaeta.

No collections were made from Low Isles of rock-burrowing Polychaeta, which undoubtedly play as important a part on this reef as they have been found to do on many others. Gardiner (1903*a*) mentions certain species of Eunicidae, Lumbriconereidae, Scoleciformia and Phyllodocidae in the order of their importance as borers from the Maldive reefs, while Crossland (1903) mentions the Eunicidae (*Eunice siciliensis* and *Lysidice collaris*) and some Cirratulidae as boring into the coral reefs at Zanzibar. The burrows of many of the above are long and winding, and the animals are difficult to extract without injury unless narcotics are employed. Most of the observations on boring are restricted to certain European species, notably *Polydora ciliata*, *P. hoplura* and *Sabella saxicava* (see Lankester, 1868; McIntosh, 1868; and Carazzi, 1893), and from these and other results the following methods have been suggested:

(*a*) Mechanical—by means of the jaws or stiff bristles on the parapodia or elsewhere.

(*b*) Chemical—by means of an acid secretion.

(*c*) A combination of both these methods.

In many collections lack of direct observation makes it doubtful if the supposed boring species collected are genuine burrowers, or ones that have crawled into burrows made by other animals or have grown up with coral colonies.

4. Gephyrea. Sipunculoidea.

Aspidosiphon steenstrupii, *Physcosoma scolops* and *Cleosiphon aspergillum*.

Rock-burrowing Sipunculids have been recognized as important factors in coral reef destruction, notably by Gardiner (1903*a*), and they certainly play a most important part in the disintegration of many of the coral rocks at Low Isles. The burrows are long and winding, and the animals are very difficult to extract without injury. Very little is known about the mode of boring, although some species have been presumed to possess an acid secretion. The three species from Low Isles, as well as the majority of presumed burrowing species collected from other reefs, have around the anterior, and often the posterior ends of their bodies, a hard longitudinally ribbed band of a chitin-like substance. As described by Gardiner (1903*a*), these animals are able to wedge themselves very securely within their burrows, and movements of these hard bands might be effective in grinding the rock away.

5. Echinodermata. Echinoidea.

Echinometra mathaei and *Echinostrephus molare.*

The literature on the boring habits in this group of animals has been reviewed and compiled by the author (1932). Cailliaud (1856*b* and 1857) and John (1889) alone give accurate details of how boring takes place, and both are agreed that the teeth and spines are the effective organs. Cailliaud describes the method of boring as follows: The body of the animal is anchored in position by means of the tube-feet, the jaw is opened and the five teeth are protruded from the buccal chamber to the required length, depending on the hardness of the rock. The five teeth strike the rock like picks, thereby dislodging fragments, and as the teeth are curved, a powerful glancing blow is ensured. If the rock is very hard the Echinoid can close its jaws to form a single bundle of its five teeth, which strike the rock as one pick. John considers that the ventral spines play some part in burrowing, these being brought into play by a rotary movement of the animal within its burrow. The teeth also assist during this rotary movement by being projected outside the buccal chamber, and being forced against the bottom of the burrow by means of the spines and tube-feet. Probably in most burrowing species a combination of the two methods takes place—deepening of the burrow by means of the teeth, both by striking and rotary action, and widening by means of the spines. The burrows of both *Echinometra mathaei* and *Echinostrephus molare* are comparatively shallow.

6. Crustacea. Cirripedia.

Lithotrya valentiana.

The pedunculate barnacle *Lithotrya valentiana* (Cannon, 'G.B.R. Exped. Reports', Vol. V, No. 1) is the only rock-burrowing barnacle found at Low Isles. The burrows are easily distinguished on the surface of the rock at low tide (Plate IV, fig. 2), being oval on the surface and approximately 1 cm. by 0·7 cm. in diameter in the largest individuals, which average about 3 cm. in length. In longitudinal section the burrow is of the same shape as the peduncle, and consequently is slightly curved inwards along the carinal margin towards the basal disc of attachment. The burrow gradually tapers towards the apex, which is rounded. At low tide the animal retracts itself into its burrow, when the top of the plates of the capitulum are brought level with the rock surface, these being frequently covered by algal growths. At high tide the animal protrudes the whole of the capitulum outside the burrow; the plates are then separated and the cirri protruded when feeding. The peduncle, as in other species of this genus, is covered with studs composed of an inner chitinous core overlaid by a calcareous covering. These studs and the basal margins of the laminae of the valves are the organs that are used for boring (Cannon, 'G.B.R. Exped. Reports', Vol. V, No. 1, Plates I and II). The whole chitinous outer skin of the peduncle is periodically cast, fresh studs taking the place of the old ones worn down in boring. The laminae of the valves each have a row of chitinous teeth along their basal margins, the basal margin of each lamina overlapping the one below it. The basal disc of attachment is calcareous and situated on the carinal margin of the peduncle. In most specimens of *Lithotrya valentiana*, as in *L. nicobarica*, a row of old calcareous discs of attachment, or their remains, can be traced down the sides of the burrow. The method of boring by

L. nicobarica is described by Seymour Sewell (1926, pp. 274–276), who states that it is the result of friction of the scales on the peduncle and the edges of the laminae of the valves against the walls of the burrow as the animal moves.

(ii) CHEMICAL BORERS.

1. Mollusca. Lamellibranchia.

The species of the genus *Lithophaga*. (Plate I, fig. 1[4–8]; and Plate II, fig. 2.)

The burrows formed by species of this genus can always be distinguished by the aperture at the surface of the rock. The aperture (Plate III, figs. 1 and 2) consists of a "dumb-bell" or "figure-of-eight" shaped hole, the two lobes of which are joined by a narrow slit-like aperture. One lobe is smaller and rather more elongated than the other. This is the opening of the inhalent siphon and is ventral in position. The inhalent and exhalent siphons are connected for their whole length, the inhalent siphon being open longitudinally along its ventral edge in continuation with the pallial edges of the mantle. The burrow (Text-fig. 2 and Plate IV, fig. 1) is often as long again as the shell, the anterior region being of the same shape, but slightly wider in diameter and almost circular in transverse section. The posterior region, that occupied by the siphons of the animal, tapers gradually posteriorly (towards the exterior) along the axes of the two siphons, which eventually almost meet, in the neighbourhood of the constriction between the two siphonal apertures. Thus posteriorly the burrow becomes more and more oval in transverse section, until a short distance before the external aperture, when a constriction appears which, becoming more pronounced, forms the characteristic "figure-of-eight" shaped aperture (Text-fig. 2). The vertical diameter at the entrance of the burrow is, however, only very slightly less than that at the anterior region. On extracting the animal from its burrow, the valves of the shell usually gape (Plate II, fig. 2) owing to the weakness of the adductor muscles, the valves being normally supported by the walls of the burrow. The foot (Plate II, fig. 2) is long and slender, its end, when extended, terminating in a spade-shaped swelling. At the base of the foot lies the byssus-gland. The byssus consists of only a few threads, which, in an individual about 4–5 cm. long, are spread longitudinally along the mid-ventral line for approximately 1 cm. By moving the ventral part of the foot the animal is able to slide up and down its burrow, even when its valves are closed, by pulling on the byssus. At low tide the shells of these species are moved up as far as possible into that region of the burrow normally occupied by the siphons, the posterior edges of the valves being often within a short distance of the exterior (Plate III, figs. 1 and 2). The burrow is thus partially closed against the entrance of enemies, while evaporation of water inside is prevented.

The species of *Lithophaga*, which occur only in calcareous rocks and possess no specializations for mechanical boring, have for a considerable time been presumed to bore by the secretion of an acid. The thick periostracum on the shells of *Lithophaga teres* (Plate I, fig. 1[4]) from Low Isles, as well as on the shells of the Mediterranean species, *Lithophaga lithophaga*, upon which all the work on the chemical boring of this genus has so far been done (Carazzi, 1892; and List, 1902), was supposed to protect the shell against the acid secretion. But in *Lithophaga cumingiana* (Plate I, fig. 1[5]), *L. obesa*

(Plate I, fig. 1[6]) and *L. hanleyana* (Plate 1, fig. 1[7]) the periostracum is comparatively thin, the shell having the following calcareous deposits outside the periostracum (text-fig. 2).

(*a*) *On the postero-dorsal region of the shell:* In *L. hanleyana* this is well developed and striated posteriorly.

(*b*) *On the antero-ventral region of the shell:* This deposit is always thin and smooth, but is present in all three species.

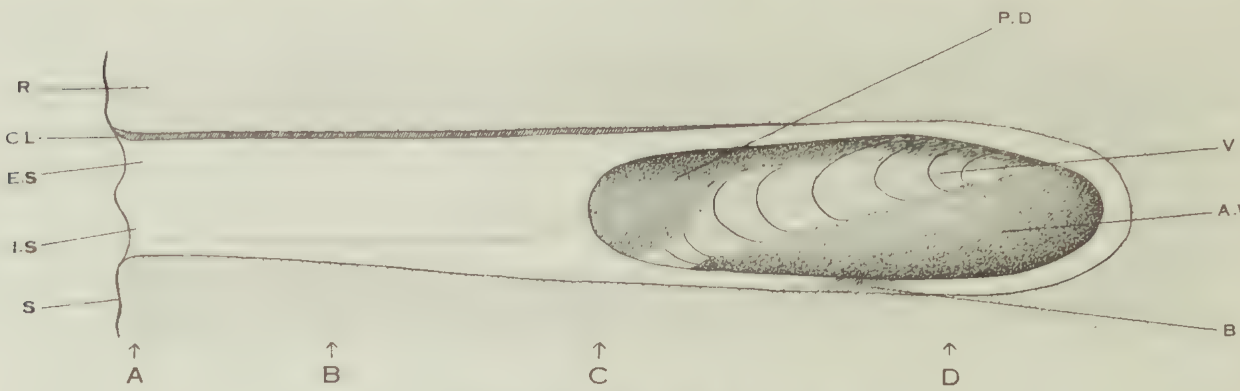
(*c*) *On the dorsal region of the shell* a soft, muddy, paste-like covering occurs in all three species, but is often absent.

The postero-dorsal calcareous deposit extends diagonally forwards and terminates slightly anterior to the hinge; anteriorly this deposit is often considerably worn down, and in places is entirely absent, leaving the periostracum uncovered (Text-fig. 2). Although thicker posteriorly, this deposit is not so smooth, or uniform, as the thin antero-ventral deposit, to which it is joined along its upper edge, on a well-defined line extending diagonally across the valves, from a point a short distance anterior to the hinge to the postero-ventral corner of the shell. In *L. hanleyana* the postero-dorsal deposit, besides being striated posteriorly, often has a V-shaped termination, the apex of the V fitting into the slit-like aperture between the two siphon tubes when the shell is moved up into the posterior region of the burrow. The whole forms a close-fitting operculum.

Around the region of the hinge the shell is covered by a soft paste-like covering which is easily removable. This is composed of calcareous matter held in place by a structureless substance, which is insoluble in dilute hydrochloric acid. Cailliaud (1856*a*) found this in some forms of *L. lithophaga*. together with the postero-dorsal calcareous covering, and considered that this latter deposit was formed of the old paste-like coverings which have become fused to this region of the valves by their outward pressure against the walls of the burrow. The paste-like covering he considered to be formed of calcareous fragments ground away from the siphonal region of the burrow by the posterior ends of the valves. Although the muddy matter contained in the paste-like covering is possibly formed as Cailliaud suggests, the postero-dorsal calcareous covering appears to be laid down by the overlapping of the tissues of the siphons upon this region of the valves, its thinning-out anteriorly being caused by the older anterior layers having received more wear than the newer posterior deposits.

The antero-ventral deposit (Text-fig. 2) is smooth, but so thin that the periostracum in many places can be seen through it. Unlike the postero-dorsal deposit it is uniform in thickness over its whole area, but from the shape of the area, like the postero-dorsal deposit, it appears to have been laid down during the growth of the animal. All species of *Lithophaga* observed at Low Isles were able to protrude the pallial border of the mantle for a considerable distance beyond the margins of the valves (Plate II, fig. 2), and the same was observed by List (1902) in the case of *Lithophaga lithophaga*. It seems reasonable to suppose that this antero-ventral deposit is laid down by the reflexing of the ventral pallial margins against the outside of the shell, thus bringing the inner fold, which lies normally against the inner ventral edge of the shell, against the outer surface.

Direction of boring is best seen in *L. cumingiana*, *L. obesa* or *L. hanleyana*, species whose siphons secrete a calcareous lining to the burrow, the presence and thickness of this lining or its absence showing the direction of boring (Text-figs. 2 and 3). In the above species this calcareous lining extends posteriorly along the dorsal and lateral surfaces of the burrow, from approximately just behind the position of the hinge, when the shell is in its normal position at the anterior end of the burrow, and only reaches the ventral surface of the burrow a short distance behind the external aperture, and this only in old individuals, where it forms a complete ring in transverse section, although much thinner ventrally than dorsally. From where it begins, anteriorly, near the position of the hinge, this calcareous lining extends diagonally downwards, becoming thinner as it extends ventrally. In transverse section across the siphon region of the burrow (Text-fig. 2) successive stages of growth can be seen as layers in this calcareous lining, the youngest



Longitudinal section of burrow.

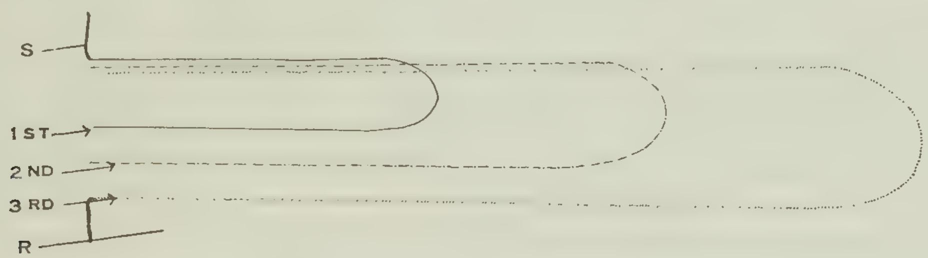
Transverse sections of burrow at A, B, C and D.

TEXT-FIG. 2. Burrow of *Lithophaga cumingiana*, in section. (Nat. size.)

AV, antero-ventral calcareous deposit; B, byssus; CL, calcareous lining; ES, exhalent siphon; IS, inhalent siphon; PD, postero-dorsal calcareous deposit; R, coral rock (coarsely stippled); S, surface of the rock; V, valves of the shell. The dotted line shows the anterior and ventral limit of the calcareous lining to the burrow.

stage being represented by a crescent of small radius at the top, overlaid by crescents of successive growths of wider radii, the latest stage of growth forming almost a complete oval, except perhaps at the extreme ventral surface. This calcareous lining is apparently secreted by the whole external surface of the siphons. List (1902) shows that the siphons are prolongations of the inner fold of the pallial edge of the mantle and, like it, have the power of secreting calcium carbonate. The direction of boring may thus be considered to take place where this calcareous lining is absent from the walls of the burrow, *i. e.* anteriorly and ventrally.

As the calcareous deposits on the valves as well as the lining to the burrow are not dissolved, and boring is not equal all around the burrow, as would occur if free acid were secreted directly into its lumen, it appears that the acid secretion is only applied directly to those surfaces of the burrow in contact with the free edges of the siphons and mantle, when these are protruded, the acid secretion being immediately neutralized by the rock before it can come into contact with the shell or any other region of the burrow. The effect of this presumed application of the acid is particularly well illustrated in burrows of *L. cumingiana* in the beach sandstone. Here each calcareous sand-grain is dissolved down to exactly the same level as its neighbour, the inside surface of the burrow being quite smooth as if mechanically bored. List (1902) found two glands in the mantle of *L. lithophaga*, whose secretion gave an acid reaction. These glands are formed by the folding of the glandular epithelium of the middle fold of the pallial edge and consist of anterior and posterior portions, the largest posterior portion being continued along the free ventral edges of the siphons. This glandular middle fold is hidden between the inner and outer folds when the pallial edge is retracted within the limit of the valves, but when protruded and reflexed



Text-fig. 3.—*Lithophaga cumingiana.* Outlines of burrows superimposed made by one, two and three year old individuals of *Lithophaga cumingiana* from the Beach Sandstone. The figure shows the direction and speed of boring which is approximately 1·5 cm. for each of the first three years (see Graph, p. 342). R, coral rock; S, surface of the rock. (Nat. size).

– – = Burrows formed by specimens one year old and approximately 1·75 cm. long.

—·—· –·—·—·— = Burrows formed by specimens two years old and approximately 3·25 cm. long.

= Burrows formed by specimens three years old and approximately 4.75 cm. long.

the middle fold is exposed and lies against the ventral region of the burrow. List considers that these glandular regions may be the organ utilized for boring, but considers that an acid reaction is not sufficient proof of this activity. However, as their position agrees with the direction of boring, as proved by those species which secrete a calcareous lining to their burrows, it seems reasonable to conclude that they are used for this purpose. The only other organ in the animal's body which can be applied to the ventral region of the burrow is the foot, but it seems most unlikely that it possesses the power of either secreting or dissolving calcium carbonate and its function is probably only for planting the byssus.

Lithophaga teres (Plate I, fig. 14) resembles the Mediterranean *L. lithophaga* in that there are no calcareous deposits on the valves and no calcareous lining to the siphonal region of the burrow (Plate IV, fig. 1). The burrow, however, in other respects resembles that of *L. cumingiana*. In this species the inner fold of the pallial edge, and its continuation to form the siphons, apparently cannot secrete calcium carbonate. *L. teres* may thus be considered to be not so specialized for rock-boring as *L. cumingiana*, *L. obesa* or *L. hanleyana*, for the calcareous lining to the siphonal region of the burrow of these species, besides forming a smooth surface for the siphons, would also help to hold rock of a fragmentary nature together around the burrow entrance. In *L. teres* the periostracum is particularly thick, and there is well-marked vertical ribbing on the antero-ventral region of the shell, corresponding in position to the antero-ventral calcareous deposit found in *L. cumingiana*, etc. This ribbing suggests that boring is in part mechanical, owing to the filing action of the shell when moved up and down the burrow, but although the hollows between the ridges are sometimes filled up with powdered rock, it seems improbable that they play a significant part in burrow-formation, as they show no sign of wear. Moreover the animal is only able to anchor itself against the ventral wall of the burrow by means of the byssus, and can thus bring little pressure to bear on this region.

In *L. argentea* (Plate I, fig. 18) the burrow is not nearly so deep in proportion as in the other species discussed, and is roughly triangular in transverse section, like the shell. The periostracum is thin and is prolonged into a fibrous extension at the pointed posterior extremity of the valves, which may help in the closing of the burrow. In some specimens a paste-like covering is found on the dorsal region of the valves, as in *L. cumingiana*. In common with *L. teres* there is no calcareous lining to the siphonal region of the burrow, and no calcareous deposits on the shell. *L. argentea* may be considered less specialized than *L. teres*.

Occasionally some curious abnormalities were found associated with peculiar habitats. The burrows of *L. cumingiana*, *L. hanleyana* and *L. teres*, when in *Acropora*-branches, were often found to curve to a slight extent, so as to bring the animal into the longitudinal axis of the branch, otherwise stunting in length would occur. When the apex of the burrow was within a millimetre or so of the exterior, as frequently happened when flat plates of *Parona*, etc., were attacked, it was usually coated over with a layer of calcium carbonate, longitudinal boring having stopped and all further growth taking place ventrally and laterally. A similar sealing over of the anterior ends of burrows was found in some large and probably old specimens of *L. cumingiana* from quite normal habitats.

Experiments were tried as to what would happen if *L. cumingiana*, *L. teres* and *Gastrochaena cuneiformis* were removed from their burrows, but all were unsuccessful. However it is here interesting to quote some recent information procured by Mr. G. C. Bertram from Guardaga in the Red Sea during 1933–34. Among his collections are a specimen of *Lithophaga*, probably *L. hanleyana*, and a *Gastrochaena* very like *G. cuneiformis*. Both had been exposed on the rock surface, and had built up new calcareous tubes around their siphons and the posterior regions of their valves. The *Lithophaga* bore the label: "These *Lithophagae* were partly exposed, since when they have formed new calcareous tubes around themselves. The new tube grows up from the adjacent remaining matrix (and does not form direct over the animal as with *Pholas*), and at first is a soft membrane in which later precipitation takes place." Whether this "remaining matrix" and "soft membrane" correspond to the dorsal posterior soft paste-like covering in *L. cumingiana*, *L. obesa* and *L. hanleyana* is difficult to determine. The *Gastrochaena* was labelled, "Exposed on surface and very rapidly (in about three days) can produce a calcareous covering such as this". It is probably only in very exceptional circumstances in nature that the animal could survive the total exposure necessary to produce the above, for the specimens which were exposed experimentally at Low Isles were almost invariably eaten by predatory fish. However, in many of the boulders on the boulder tract, some of the original specimens of *L. cumingiana* succeeded in burrowing further into the rock matrix after the erosion of their calcareous siphon tubes during the transit of the boulder to its present position from deep water. In these specimens the siphons filled up the enlarged opening, leaving the tubes of the original burrow as a jagged margin around their present apertures (Plates IV, fig. 2, and VI, fig. 1).

Modiolus cinnamomeus. (Plate I, fig. 1^{9}.)

The genus *Modiolus* only differs from *Lithophaga* in the shape of the shell, the rest of the anatomy being practically identical, as far as is known. As in *Lithophaga*, the mantle and inhalent siphon are open along the ventral edge for their whole length, but the siphons are in proportion not so long. The burrow is comparatively shallow and kidney-shaped like the shell, and like those of *L. teres* and *L. argentea* is completely unlined, nor are there any calcareous deposits on the outer surfaces of the valves. The entrance to the burrow is also roughly figure-of-eight shaped. On account of the near relationship of this genus to *Lithophaga*, and the absence of any specializations characteristic of mechanical borers, it is reasonable to presume that boring takes place by chemical action, and that acid-secreting glandular regions probably exist in the middle fold of the pallial edge of the mantle and inhalent siphon, although not so well developed as in *Lithophaga*.

The rock-burrowing filibranch Lamellibranchs, species of *Lithophaga* and *Modiolus* mentioned above, can thus be arranged in order of their degree of specialization for rock-burrowing, beginning with those having the simplest burrows and ending with the most complex :

1. *Modiolus cinnamomeus* and *Lithophaga argentea.* (Plate I, fig. $1^{9, 8}$.)

   The burrows are shallow, the shell being only just below the surface, and there is no calcareous lining to the siphon-tubes and no deposit on the shells.

   These species appear to be the least specialized.

2. *Lithophaga teres.* (Plate I, fig. 1^{4}.)

   The shell is bare like *L. argentea*, but the burrow is deeper and typical of this genus. *L. lithophaga* from the Mediterranean can be included here.

3. *Lithophaga cumingiana* and *L. obesa.* (Plate I, fig. $1^{5, 6}$, and Plate II, fig. 2.)

   The burrows are typical, and the siphon-tubes and posterior region have a calcareous lining. There are calcareous deposits on the shell, but posteriorly these are not sufficiently developed to form a close-fitting operculum to the burrow.

4. *Lithophaga hanleyana.* (Plate I, fig. 1^{7}.)

   The burrow and deposits on the shell are similar to those of the last two species. The posterior calcareous deposit on the shell, however, is thicker, and forms a close-fitting operculum to the burrow. This species appears to be the most specialized, and it is interesting to note that this is the only *Lithophaga* which is found at all commonly in living coral colonies at Low Isles.

2. Porifera.

Spirastrella inconstans and *S. aurivillii.*

The rock-burrowing sponges are among the most important organisms concerned with coral reef disintegration. Superficially their effect on rocks is inconspicuous; there are no large entrances to the burrows on the rock surface, the ostia communicating with the exterior being usually minute and often hidden by superficial sponge or algal growth. But internally the infected rock is frequently found to be completely rotten, and sometimes quite vesicular with cavities made by these animals. The Clionidae and Spirastrellidae, families of the group Clavulinae, are the most important in this respect (see the works of Topsent, especially 1887; Annandale, 1915*a* and *b*; and Cotte, 1902), but many of them are only rock-burrowers in their early stages. The burrows vary considerably; some are in the form of large cavities, as in the above species, while others form fine ramifications through the interstices of the rock. The burrowing is almost certainly due to chemical action, although a mechanical method, depending on growth pressure and movement of the spicules, has been suggested by Annandale (1915*b*).

3. Algae and Fungi.

Certain green (Chlorophyceae), blue-green (Cyanophyceae) and red algae (Rhodophyceae), and some fungi, have been recorded as making impressions on or burrowing in calcareous rocks, mollusc shells, corals, and in fact in almost all calcareous matter except Echinoid tests (see Kölliker, 1859; Duncan, 1876; Bornet and Flahault, 1889; Johnson, 1894; and Duerden, 1902). Many undoubtedly occurred at Low Isles as they do on all coral reefs. These burrowing plants, although superficially inconspicuous, play one of the most important parts in coral reef destruction. Many are quite superficial, making only shallow pits or impressions, which are visible as a green coloration on the deeper parts of many "living reef" corals, while others, saprophytic species, form fine ramifications deep into the rock like some of the Porifera. The most important of these plants is *Achyla penetrans* (Duncan, 1876), which was at first supposed to be a fungus (Saprolegniaceae), but later was identified as consisting of several species of green and blue-green algae. The method of burrowing is undoubtedly by chemical means, by the action of carbon dioxide produced by respiration, as suggested by Kölliker (1859), Duncan (1876), and Duerden (1902), but in some species other acids may possibly be used. Bourne (1893) found that a certain boring green alga, together with some Porifera (Clionidae), play an important part in the separation of the young individuals of *Fungia* from the parent stem.

B. FEEDING AND GROWTH IN RELATION TO ROCK-BORING.

The main factors that distinguish rock-boring animals from wood-boring forms are that, whereas some of the latter, such as *Teredo* and *Bankia*, bore for food as well as for protection, the former bore only for protection or to keep moist at low tide. The speed of boring in rocks is probably always extremely slow, and usually in direct proportion to the rate of growth. Some of the boring Polychaetes, such as the British *Polydora* *ciliata*, are believed to use their jaws for boring, and, as McIntosh (1868) states, pass the material thus obtained through the alimentary canal. It is possible that they obtain some nourishment by devouring boring sponges and algae, whose tissues ramify for considerable distances through the rock. Many rasping and browsing animals also remove the surface layer of the rock along with the superficial algal growth, and, as already mentioned, the calcareous faeces of the chiton, *Acanthozostera gemmata*, show that some of the rock substance is swallowed. As regards the rock-burrowing Echinoids, Cailliaud (1857), John (1889) and Hesse (1867), all of whom worked on *Strongylocentrotus lividus*, state that this Echinoid passes the material that it bores through its alimentary canal, but no indication is given as to the nature of the food, if any, that it obtains by these means. Other burrowing species of Echinoids may possibly ingest the rock, and there appears no reason why a little nourishment should not be obtained as in the case of certain browsing animals and rock-burrowing Polychaetes, and especially when burrowing into *Lithothamnion*. All the rock-burrowing Lamellibranchs feed by means of ciliary currents on phytoplankton in common with other members of that group. In those species that bore mechanically it may be possible for some of the pulverized rock to be sucked through the pedal orifice onto the gills or palps. The boring Sipunculids feed by means of ciliated tentacles situated around the mouth, the mouth being placed at the anterior extremity of a long introvert, which in the boring genera *Cleosiphon*, *Aspidosiphon* and *Physcosoma* is extended from a position considerably behind the anterior end of the animal. The anus is situated in the same region. As described by Gardiner (1903*a*), the average diameter of the burrow of these animals is not more than one-half to one-third the diameter to which the animal expands when extracted from its burrow. The animal has thus a very tight fit within the burrow, and its introvert could not possibly be extended when the animal is *in situ*. When feeding it must come to the entrance of its burrow and extrude that region of its anterior end bearing the introvert. Finckh (1904) makes the not very comprehensible statement that he has seen these animals feeding on *Lithothamnion* surrounding their burrows at Funafuti. But beyond mentioning the possession of a long retractile proboscis he does not state how they do this. The rock-burrowing barnacle *Lithotrya valentiana* catches food by means of its cirri like other members of the Lepadidae. The various families of boring sponges may be presumed to feed in a typical manner, and even those which excavate cavities deep in coral rock have ostia communicating with the exterior.

Duncan (1876) believes that what he terms the "organic basis" in coral rock ("a relic of an involution of the dermal structures in and around which the sclerenchyma was deposited") might provide food for certain rock-boring plants (fungi or saprophytic algae). It is, however, doubtful if this is of any value to rock-boring animals. The organic nature of this "basis" is also mentioned by Ogilvie (1896) and Bourne (1899). But Bourne, who mentions the presence of *Achyla* in many of the corals which he examined, does not state if this plant occurs more commonly in the presence of this organic matter than elsewhere.

The rate of growth, and consequently the speed of burrowing, is well shown among the Lamellibranch borers of the genus *Lithophaga*. Many of the filibranch Lamellibranchs have a very definite breeding season lasting over a comparatively short period of time, which in *Lithophaga cumingiana* occurs in March and April. In the beach sandstone on the N.E. beach of Low Isles, *Lithophaga cumingiana* grows at an average of 1·5 cm. per year for the first three years, about 330 specimens being measured for length and plotted in half-centimetre divisions (see Text-fig. 3, p. 337, and Text-fig. 4). The three peaks on the graph show the average size of presumably one- to three-year-old individuals.

TEXT-FIG. 4.—Graph showing the growth rate of *Lithophaga cumingiana*.

In the case of this rock-burrowing genus the growth of one individual does not affect that of its neighbour, as each individual inhabits a separate burrow. In the case of other Filibranch Molluscs, however, such as those species of *Mytilus* or *Modiolus*, which live in crowded conditions, those above obtain the bulk of the food, while those below are often stunted in growth.

IV. THE DISTRIBUTION AND ECOLOGY OF ROCK-BURROWING ORGANISMS

The primary factors governing the distribution of rock-burrowing organisms are as follows :

(*a*) The Physical Factors of the Environment.

The most important of these are temperature, water currents and tidal rise and fall. This latter reached about 10 ft. at springs and 2 ft. or less at neaps (Stephenson and others ' G.B.R. Exped. Reports ', Vol. III, No. 2, p. 22).

(*a*) The Geological Nature of the Rocks Available for Attack.

At Low Isles all the rocks were calcareous, and the only information regarding non-calcareous rocks was from the mainland beaches in the immediate neighbourhood, where the basalt boulders appeared to be quite free from rock-borers.

(*c*) The Nature of the Various Protective Surfaces upon Rocks.

Under this heading are included all the organic surfaces which protect rocks from the attack of boring-organisms, and the agencies by which these are removed.

A. THE VERTICAL DISTRIBUTION OVER A TIDAL AREA.

Rock-burrowing animals and plants, like many other sedentary marine organisms, are limited vertically in their distribution by the tide, some forms being able to withstand long periods of exposure at low water, while others can hardly withstand exposure at all. Taken as a whole, however, an animal in a stone burrow is not nearly so subject to changes in its external environment as animals in other habitats ; for instance water can be held in the burrow at low tide, or the burrow may be partially closed by the shell (*e. g. Lithophaga*, especially *L. hanleyana*), or a portion of the body (*e. g.* the Gephyrean borers) may act as an operculum. Most of the burrowers were found to begin at a certain vertical limit and appeared to extend downwards without a break. No information was obtained as to the lower limit of any of the animals concerned.

At Low Isles the effect of favourable and unfavourable conditions on the vertical limit of some of the rock-burrowing mollusca is very noticeable on the beach-sandstone around the beaches of the main island. Here this formation, which has a gradual slope seaward, is at a comparatively high level (Stephenson and others ' G.B.R. Exped. Reports ', Vol. III, No. 2, p. 36). On the north and north-east beaches of the island the upper 12 ft. or so of this formation iscompletely bare of rock-burrowers, although certain barnacles and rock-oysters (*Ostrea mordax*) are common ; below this is a well defined zone of *Lithophaga cumingiana* about 3–6 ft. in width (Plate III, figs. 1 and 2), at such a level as to be just awash at low-water neap tides. Below this zone the formation extends for an average of 4 ft., and eventually ends in a shallow moat. This last 4 ft. is practically devoid of *L. cumingiana*, as the surface is covered with a dense protective growth of a green alga, while all the area above this last 4 ft. is kept clean by tidal currents and wave action. It can thus be decided that the top of this particular zone of *L. cumingiana* is the highest horizon that can be inhabited by this Lamellibranch. The three small areas of beach-sandstone on the south beach of the island have approximately the same width and slope seawards, but there the rock is not kept so clean, and silt is often deposited, with the result that *L. cumingiana* is rare even at the corresponding zone at which it occurs so commonly on the north and north-east beaches. *L. cumingiana* occurs from the same vertical limit on the raised boulders on the reef edge and on the coral shingle banks. *L. teres* and *L. hanleyana* occur from a slightly lower limit, while *L. obesa* is only found at very low tide, mostly in boulders on the reef edge and in dead coral rock in the anchorage. *L. argentea* and *Modiolus cinnamomeus* are too uncommon for any idea to be formed of their vertical limit. The species of *Gastrochaena* appear to occur from a level just below that of *L. cumingiana*. *Petricola lapicida* occurs from about the same limit, but is rarely found outside the beach sandstone, the loosely cemented texture of this rock being possibly more suited to its mechanically-made burrows than the more consolidated coral rock. The rock-burrowing Sipunculids occur from approximately the same upper level as *L. cumingiana*, but the Polychaeta and Porifera have a decidedly lower limit. The barnacle *Lithotrya valentiana* occurs only sparingly in a definite zone about 1 ft. 6 in. deep on the larger coral boulders on the reef edge and "boulder zone", associated with other barnacles just below the well-defined zone formed by the rock oysters (Plate IV, fig. 2). Beds of these barnacles were not found at Low Isles, as is the case in *L. nicobarica* (Sewell, 1926), and the burrows occurred in all positions, and not only hanging vertically downwards as in *Lithotrya dorsalis* (Gardiner, 1903*a*).

Many of the coral boulders on the boulder tract (Plate VI, fig. 2) have been cast up from possibly considerable depths by past storms, and are riddled by old and weathered burrows of *Lithophaga obesa*, *L. teres* and *L. cumingiana* (Plate V, figs. 1 and 2, and VI, fig. 1). In suitable positions on these rocks a few of the original specimens of these Lamellibranchs have managed to survive, and if the rock surface has been fractured or severely weathered during or after its transit to its present position, some have sealed over their broken siphon tubes and burrowed further into the rock (Plate IV, fig. 2, and V, fig. 2). The majority have, however, perished, even when in apparently favourable positions, many probably having been devoured by predatory animals which have entered the enlarged or broken burrows, others having been washed or fallen out of their burrows during transit. In some of the original burrows old shells can still be found, the animals having probably perished by being transported above their vertical range. In many cases the upper regions of these boulders have been covered by a secondary fauna of rock oysters and barnacles (Plate V, fig. 2, and VI, fig. 2), and in some places a second attack by burrowing Lamellibranchs (*L. teres*, *L. cumingiana* and *L. hanleyana*) is now going on among the original burrows, the calcareous siphon-tubes of which, being formed of more compact calcium carbonate than the surrounding boulder, project as jagged ridges and points above its eroded surface.

The distribution of the two species of rock-burrowing Echinoids is dealt with in the expedition's ecological reports (Stephenson, and others 'G.B.R. Exped. Reports', Vol. III, No. 2), *Echinometra mathaei* occurring on the outer rampart and mangrove flat, and *Echinostrephus molare* on the seaward slopes and anchorage, while Manton ('G.B.R. Exped. Reports',. Vol. III, No. 10, Plate IV, graph 40) gives the distribution of the rock-burrowing clam *Tridacna crocea*, from the reef-flat seaward to beyond the boulder tract.

B. THE GEOLOGICAL NATURE OF THE ROCKS AVAILABLE FOR ATTACK.

According to Stephenson and others ('G.B.R. Exped. Reports', Vol. III, No. 2, p. 101), there are four types of coral rock occurring at Low Isles :

1. Beach-sandstone.
2. Shingle conglomerate.
3. Coral rock.
4. Honeycomb-rock.

In this paper honeycomb-rock, a localized type of coral rock, is included under the heading of "coral rock", while the attack by boring organisms upon loose coral shingle is described under "shingle conglomerate", its cemented form. All the above are calcareous, but the beach-sandstone contains a small percentage of siliceous and other material incorporated within it.

(i) Beach-Sandstone (Stephenson and others 'G.B.R. Exped. Reports', Vol. III, No. 2, Plate V, fig. 2).

On account of the very limited extent and comparatively high tidal horizon of the beach-sandstone (Stephenson and others 'G.B.R. Exped. Reports', Vol. III, No. 2, p. 36), many members of the rock-burrowing fauna are absent. The rock itself varies in hardness considerably, both on account of its degree of cementation as well as the hardness of its individual ingredients ; in places it is so insecurely cemented that it can be crumbled to pieces in the hand. The beach sandstone consists of coral sand, shell fragments, Foraminifera tests and many other components of various degrees of hardness cemented together by a calcareous cement. Its variation in hardness and coarse texture appear to make it unfavourable to certain mechanical burrowers such as the thin-shelled Lamellibranch *Gastrochaena*. These conditions are not unsuitable, however, to burrowers using chemical methods, such as *Lithophaga*, or to the thick-shelled Lamellibranch mechanical burrowers *Petricola*, *Arca* or *Tridacna*. *Lithophaga cumingiana* and *Petricola lapicida* are particularly common in certain regions, while *L. teres*, *L. hanleyana*, *Tridacna crocea* and Sipunculids occur sparingly in the lower horizons.

(ii) Shingle Conglomerate and Coral Shingle (Stephenson and others, 'G.B.R. Exped. Reports', Vol. III, No. 2, Plate XI, figs. 2 and 3 ; Plate XII, figs. 1 and 2 ; and Plate XIII, figs. 1 and 2).

Large areas of coral shingle occur as banks or ramparts around the east, south-east and south sides of the Low Isles reef above its living edge (Stephenson and others, 'G.B R. Exped. Reports', Vol. III, No. 2). In certain places this coarse shingle is loosely cemented together to form flat slabs of shingle conglomerate, but most of it is loose and subject to a slight movement by the waves at high tide. This keeps the shingle fragments comparatively free from attack by burrowing organisms as well as from protective animal and plant growths. In favourable places, however, it is attacked by Algae, Sipunculids, Porifera and Lamellibranch Mollusca, these latter often showing distinct stunting in growth and sometimes curving of the burrow, due to the limited space (such as *Acropora* branches) in which they live. *Lithophaga cumingiana*, *L. hanleyana* and *L. teres* are the commonest Lamellibranchs, but are all well below average size. *Gastrochaena* is very rare. Obviously such a habitat as this is quite unsuitable to the rock-burrowing Echinoids and the surface-burrowing Mollusca such as *Tridacna*, *Acanthozostera*, etc.

(iii) Coral Rock and Honeycomb Rock (Plate VI, fig. 2, and Stephenson and others, 'G.B.R. Exped. Reports', Vol. III, No. 2, Plate V, figs. 3 and 4).

Coral rock consists primarily of boulders of varying shapes and size composed of dead colonies of compact-textured corals with small calices such as *Porites*, and coarse-textured corals with large calices such as *Favia*. These boulders may be loose on the reef platform, such as on the boulder tract, or cemented down in their position of growth. The honeycomb rock (see Stephenson and others, 'G.B.R. Exped. Reports', Vol. III, No. 2, p. 93) is similar in constitution. The attack upon living coral colonies is dealt with elsewhere.

It is impossible to form any idea of the extent to which coarse and compact-textured coral boulders are attacked by mechanical burrowers, as so much depends on their degree of hardness. Texture is often of only secondary importance, hardness being mainly due to the thickness of the walls of the individual calices and to the absence of rock-burrowing sponges and plants. The length of time that a boulder is exposed to the atmosphere at low tide also appears to affect its hardness, a water-sodden boulder of *Porites* being in places very soft. Dead blocks of *Porites*, although of very compact texture, are often softer than boulders of the more open-textured Astrean corals, the walls of the calices of this latter type being often very thick and hard. This factor of the relative hardness and texture of coral boulders is, however, of no importance to burrowers using chemical methods, such as the filibranch Lamellibranchs, but is an important factor in governing the distribution of the thin-shelled Lamellibranch mechanical burrowers such as *Gastrochaena*, which is certainly more frequent in the softer and more compact-textured rocks. The rock-burrowing Polychaeta are also more frequent in the softer rocks, especially in those that are disintegrating under the effects of the burrowing sponges and plants. *Lithotrya valentiana* attacks all boulders irrespective of hardness or texture within its narrow zone of distribution, while the burrowing Sipunculids, sponges and plants appear to be equally distributed under suitable conditions in every kind of rock over the whole tidal range. The two species of rock-burrowing Echinoids, and the species of *Tridacna*, *Arca* and *Acanthozostera* are also quite unaffected by the hardness and texture of the various coral boulders.

(iv) Living Coral Colonies.

Rock-burrowers are uncommon in living coral colonies, on account of the protective surface of living polyps, and attack can only be possible where areas have died. Only *Lithophaga hanleyana* occurs at all commonly, and that mostly in colonies of massive *Porites*; the serrated posterior ends to its valves, which act as an operculum, possibly prevent the sealing up of its burrow by the regrowth of the coral. *Lithophaga cumingiana* and *Gastrochaena laevigata* have also been found in living coral colonies, but very rarely.

Of all the workers on coral reefs in the past, only Gardiner (1903*a*) gives detailed information concerning the ecology of rock-burrowing animals and plants. For a general comparison of their distribution over a far wider area than at Low Isles, a brief summary is given here of his observations from the reefs of the Maldive and Laccadive Islands. *Achyla* and *Cliona* were rarely found in dead or rotten coral, but appeared to riddle the coral skeleton as soon as it was laid down, and then to die with the coral, and he considers their importance mostly to lie in weakening the rock for other boring organisms. A second boring sponge, a Myxospongid, formed large cavities in coral rocks, but preferred those of perforate corals such as *Madrepora*. *Lithophaga* was very common on the reef of the island of Hulule, to the south-east of North Male Atoll, in all kinds of coral rocks, but on the reef at Minikoi it was only found once. Sipunculids were more abundant in living coral than in dead boulders, but only occurred at the base of the branches in branched forms, and were commoner in lagoons than on seaward slopes. The rock-burrowing Polychaetes were found to be most important, attacking all kinds of coral rock in every position, but preferring those of fine texture. They were the principal agents in the rotting of corals on the reef flats. The various species of Sabellids and Terebellids, which grow up with living coral colonies, he considers are important by making the corals brittle, and in affording a foothold in their tubes for more destructive burrowers.

c. THE NATURE OF THE VARIOUS PROTECTIVE COVERINGS UPON ROCKS AND THE AGENCIES WHICH REMOVE THEM OR PREVENT THEIR DEVELOPMENT.

Protective surfaces consist of—

1. A layer of sediment. This probably forms an efficient barrier against the attack of the majority of boring organisms, both in the larval or adult forms, except perhaps to certain of the Polychaeta and Gephyrea.

2. The movement of rock fragments by wave action (such as on the seaward slopes of the shingle ramparts at Low Isles). This action, besides preventing the settlement of many free-swimming larvae, also keeps the rock fragments free from protective coverings.

3. A dense growth of Algae, Sponges, Barnacles and Lamellibranchs (*Ostrea mordax*, *Chama jukesii*, *Spondylus ducalis*, etc.). Although this type of protective covering may be a guard against many burrowing animals which need a clean rock surface for the attachment of their free-swimming larvae (*e. g.* the burrowing Lamellibranchs), it may be no protection whatever against other burrowing animals whose method of attack in the early stages is quite different. Rocks were often found to be completely rotten underneath owing to boring sponges, Gephyrea and Polychaeta, although fully protected against burrowing Lamellibranchs by a superficial growth of seaweed. Living calcareous algae do not appear to protect rocks, except that their growth may seal over certain burrows. The action of *Lithothamnion* as a protection to rocks was not observed at Low Isles. At Funafuti, Finckh (1904) found the rock to be much bored in certain localities, mostly by Sipunculids. He considers it to be a destroyer of living coral by smothering it.

4. Coral polyps. Coral polyps appear to form a protection against almost all burrowing organisms except certain algae, and the underlying skeleton only appears to be attacked in places where polyps or large areas of polyps have died, been eaten or otherwise

removed. The layer of living polyps catches and devours as food all free-swimming larvae (Mollusca, Polychaeta, Gephyrea and Crustacea) which happen to come near them. Even when dead areas are attacked many burrowing animals eventually perish by the sealing up of their burrows by the regrowth of the coral. There is no evidence that any of the larvae of boring animals are capable of killing coral polyps and thus infecting living coral direct.

Agencies which produce clean rock surfaces favourable for the attachment of the free swimming larvae of rock-burrowing Lamellibranchs and certain other borers :—

1. Wave and current action. Waves, and to a lesser degree currents, besides moving loose shingle, in certain places also prevent the formation of protective surfaces, such as silt and certain organisms ; in times of storm clean coral boulders are often torn from the sea bottom, and cast into favourable positions for attack.

2. Agencies which periodically kill coral colonies and are later themselves removed. These include temporary layers of silt, excessive rain at periods of low tide, the extensive growth of some seaweeds at certain periods of the year, which later die, and perhaps in a few places near the mainland the lowering of the salinity of the sea-water owing to the flood-waters of rivers.

3. Browsing animals which feed on superficial algae and living coral polyps. Under this heading are included all those animals (mostly Gastropoda, Amphineura and Echinoids) which feed on the superficial layer of algae growing upon rocks. Several of these (Echinoids and Amphineura, etc.) rasp away the topmost layer of rock, and some are able to make shallow burrows for themselves on the rock surface. The animals which feed on living coral polyps expose clean areas of rock for the settlement of the larvae of other burrowing organisms. The most important of these are certain fish of the genus *Pseudoscarus* and some Gastropods. Gardiner (1903*a*) mentions a Gastropod from the Maldives which feeds on living coral and leaves dead trails in its wake, but at Low Isles Stephenson found that living coral was rarely attacked.

TABLE I.—*Distribution of the Rock-burrowing Mollusca, Echinoids and Lithotrya from Certain Localities on the Reef at Low Isles.*

The table is based on personal observations and those of Stephenson and others, 'G.B.R. Exped. Reports', Vol. III, No. 2.

Name.	Living coral colonies	Beach sand-stone.	Shingle ramparts.	Boulders reef flat.	Boulders boulder tract.	Outer boulders and seaward slopes.
Lithophaga cumingiana	very rare	very common	53·0	15·6	16·7	18·3
L. obesa	..	..	..	0·8	0·5	12·8
L. hanleyana	×	very rare	10·7	7·6	18·3	14·7
L. teres	..	..	12·4	19·7	31·6	23·9
L. argentea	..	..	2·8	2·8	..	..
Modiolus cinnamomeus	..	..	6·0	10·4	2·2	1·85
Arca imbricata	..	..	..	..	×	×
Gastrochaena cuneiformis	very rare	common	11·3	27·8	18·8	23·0
G. laevigata	..	rare	2·3	3·8	6·1	4·6
Petricola lapicida	..	common	0·06	3·8	1·0	0·9
Tridacna crocea	..	rare	..	×	common	×
T. maxima var. *fossor*	..	..	..	×	..	×
Acanthozostera gemmata	..	×	×	×	×	×
Echinometra mathaei	..	..	..	×	×	×
Echinostrephus molare	..	..	..	..	..	×
Lithotrya valentiana	..	..	..	..	×	×

Where large collections were made of burrowing Lamellibranchs the approximate relative abundance of species is given as a percentage of the total for the particular habitat ; other species occurring are indicated by a cross.

V. THE DESTRUCTIVE EFFECTS OF ROCK-BURROWERS IN RELATION TO CORAL REEFS

The destructive effect of rock-burrowers can be conveniently tabulated under two headings :

(*a*) *The Direct Effect.*

Under this heading is considered the effect of burrowers in removing the rock which they bore away when forming or enlarging their burrows. With mechanical borers this is usually removed in a pulverized state or a fine mud, although some of the Clionidae (Annandale, 1915*a* and *b*) are considered to break off comparatively large fragments, while by the chemical borers the rock is removed in solution. According to other workers, especially Gardiner, who has observed the effects of these organisms over a wide field, the volume of rock removed directly by boring organisms may be very considerable in some localities. At Low Isles this effect appeared comparatively insignificant. Owing to the abundance and general distribution of burrowing algae, and possibly also certain bacteria, the direct effect of chemical burrowers is probably far greater than that of mechanical borers in any locality.

(*b*) *The Indirect Effect.*

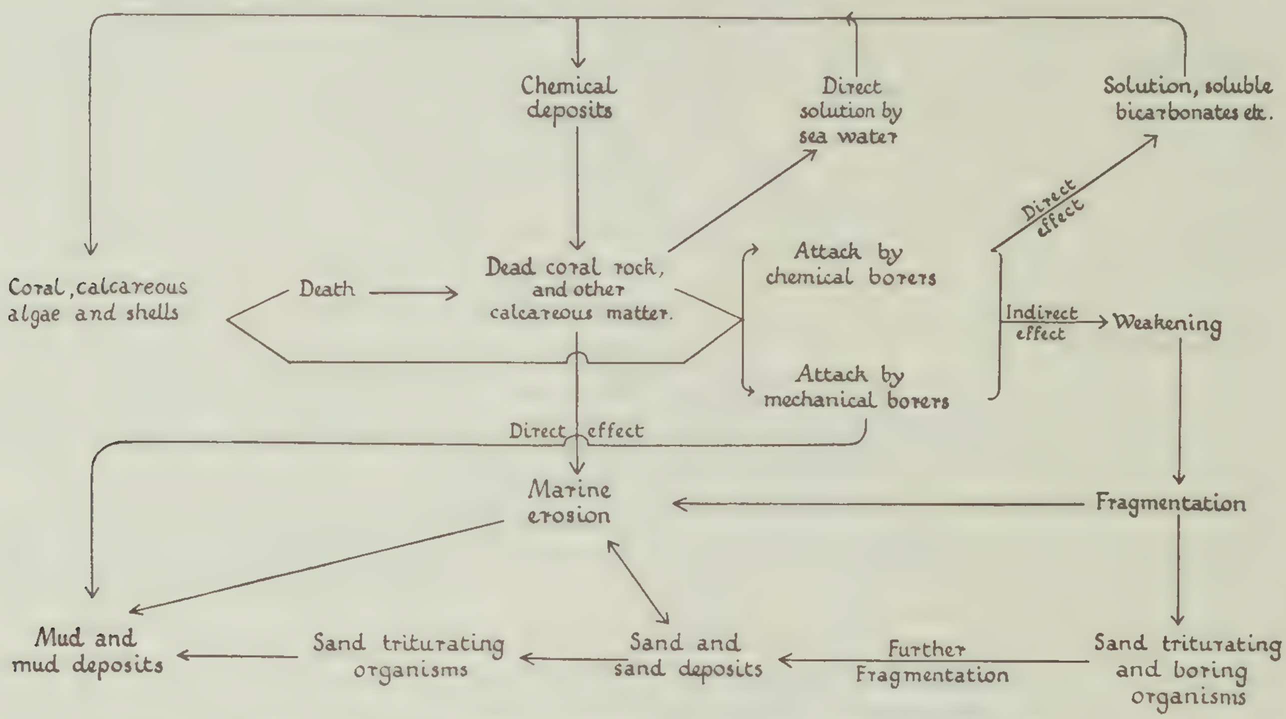
Under this heading are considered the effects of rock-burrowers in aiding marine erosion, the combined results of which are undoubtedly one of the most important factors in coral reef destruction. These may be tabulated as follows :

(1) Weakening of the rock structure by the burrows, especially of the Algae, Porifera, Polychaeta and Sipunculoidea. These unlined burrows make the rock comparatively weak and more prone to fragmentation. The burrows which are lined with calcium carbonate, as in many Lamellibranchs and some Polychaetes (fanworms, etc.), do not appear to be so detrimental to the mechanical structure of the rock as do unlined burrows. In the case of *Lithophaga* the calcareous lining laid down by the siphons is a more dense form of calcium carbonate than the surrounding rock and appears to bind the rock together, Some of the boulders on the Low Isles boulder tract were in an advanced state of decay. But many of the old *Lithophaga*-burrows were intact and little eroded. A more emphasized but somewhat analogous case could be seen in the mangrove swamp at Low Isles, where logs of mangrove wood had almost completely rotted away, but their original shape persisted in the maze of winding calcareous tubes laid down by hundreds of *Teredo*. Gardiner (1903*a*), however, states that Polychaetes (fanworms, etc.) which grow up with living coral colonies make these brittle.

(2) The burrows of many of these organisms considerably increase the rock area, offering clean rock-surfaces for further attack by other borers and for the direct solution of the rock by sea-water if this can still be considered an important factor in the destruction of calcareous rocks.

(3) The empty burrows, especially the shallow depressions formed by Chitons and Echinoids, etc., in some localities become centres for the collection of sand and fine stones which under wave- and current-movement exert an abrasive action on the surrounding rock.

Gardiner, who has examined very many reefs, has come to the conclusion that rock-boring organisms are one of the main factors in the destruction of coral reefs. He gives (1903*b*) the following order of their attack on coral rock: first boring Algae, then the Porifera, Polychaeta (especially *Eunicidae*), Sipunculids (*Aspidosiphon*, etc.), and *Lithophaga*. The rock is eventually broken up into fragments and then into sand, which in turn by the action of sand-triturating animals is converted into mud. Finckh (1904) also considers boring organisms of some importance and states: "To what extent destruction of the reef rock by these agencies [boring organisms] is going on was not ascertained, but in course of time it must be considerable. Indeed, were it not for [the cementing action of] the *Lithothamnion*, localities such as the ocean platform of the Island of Funafuti, where there is so little other growth, would be undergoing decided diminution."



TEXT-FIG. 5. The cycle of events in the destruction of a Coral Reef.

On the other hand, Wood Jones (1910) at Cocos Keeling Atoll tends to consider the effects of boring organisms as slight, on account of the relative unimportance of both their direct effect and in destroying living coral. He states: "There seems to be indeed an almost symbiotic relationship between certain boring animals and the corals that they have chosen as their hosts, for coral growth extends and strengthens their tubes by sympathetic growth, and the cavities of the Molluscs in many cases expand the living area of the surface of corals by causing irritation and repair."

Although they are not concerned with the subject under discussion in this present paper, mention must be made of those organisms which further break up coral rock after its fragmentation by marine erosion aided by boring organisms. These animals, by digesting the organic matter among and around rock fragments and coarse sand, triturate the fragments and sand into finer and finer particles on their passage through the alimentary canal, much in the same way as earthworms pulverize the particles of soil which they have eaten. In the Maldives Gardiner (1903*a*) found these animals to be one of the primary causes of the conversion of coral sand into mud, and places the Holothurians foremost in importance in this respect, followed by certain Sipunculids and Polychaetes. Finckh (1904) at Funafuti, on the other hand, disregards the triturating action of the Holothurians and states: "They were, however, continually feeding on the coarse sand, which, as was seen from the sausage-shaped excrements, left them (so far as could be ascertained by the naked-eye examination) in the same condition as that in which it entered." At Low Isles the effect of these animals was not examined, but there seems no reason to doubt that here, as in the Maldives, certain Holothurians, perhaps not all the sand-feeding species that occurred, and probably many Polychaetes and Sipunculids, do play some part in the further conversion of coral sand into mud.

Text-fig. 5, adapted from these and Gardiner's observations, shows roughly the cycle of events in the destruction of a coral reef.

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DESCRIPTION OF PLATE I.

FIG. 1.—Rock-burrowing Lamellibranchs. Natural size. Arranged in the order in which they are mentioned in the text. 1. *Petricola lapicida* Gmelin. 2. *Gastrochaena cuneiformis* Spengler. 3. *Gastrochaena laevigata* Deshayes. 4. *Lithophaga teres* Philippi. 5. *Lithophaga cumingiana* Reeve. 6. *Lithophaga obesa* Philippi. 7 *Lithophaga hanleyana* Reeve. 8. *Lithophaga argentea* Reeve. 9. *Modiolus cinnamomeus* Brugière.

FIG. 2.—A piece of coral rock split open to show a specimen of *Gastrochaena cuneiformis, in situ* within its burrow. The ventral surface is uppermost, the retracted siphons, the mantle and the foot protruding through the pedal orifice, can be seen. An old burrow of *Lithophaga teres*, with a dead shell still in it, is alongside.

1 6
2
3 7
4 8
5 9

FIG. 1.

FIG. 2.

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DESCRIPTION OF PLATE II.

FIG. 1. *Gastrochaena cuneiformis*, *in situ* within its burrow, which has been split open longitudinally, showing the length which the burrow and siphons sometimes attain. The siphons are retracted within the shell, and the calcareous lining secreted onto the burrow by their extremities can be clearly seen.

FIG. 2. Living specimens of *Lithophaga obesa*, ventral view. On the left the valves are closed, and on the right they are open, showing the retracted siphons, the wide pallial borders of the mantle, and anteriorly the foot. (Natural size.)

FIG. 1.

FIG. 2.

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DESCRIPTION OF PLATE III.

Figs. 1 and 2. Burrows of *Lithophaga cumingiana* in the beach-sandstone, showing the characteristic apertures of the burrows and in some the calcareous lining secreted by the siphons. Some of the shells can be seen to have been moved up into the posterior region of the burrow in order to block its entrance.

FIG. 1.

FIG. 2.

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DESCRIPTION OF PLATE IV.

Fig. 1. A piece of coral rock split open to show four burrows of *Lithophaga teres*. (One half natural size.)

Fig. 2. Near view of a portion of a boulder on the Boulder Tract showing *Ostrea mordax*, barnacles, old and inhabited burrows of *Lithophaga* and *Lithotrya valentiana*.

FIG. 1.

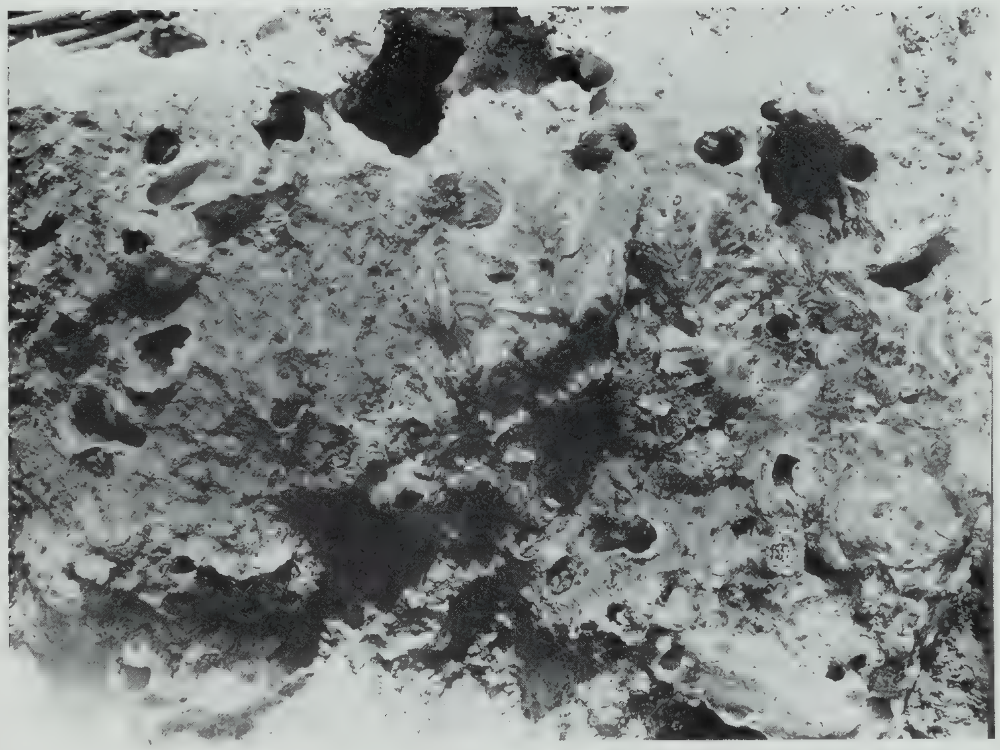

FIG. 2.

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DESCRIPTION OF PLATE V.

FIG. 1. Near view of a portion of a boulder on the Boulder Tract showing a protective covering of *Ostrea mordax* above and old *Lithophaga* burrows below.

FIG. 2. Near view of a portion of a boulder on the Boulder Tract showing many old burrows of *Lithophaga cumingiana* and *L. obesa*, and the calcareous lining to the siphon tubes, which project above the eroded surface of the rock.

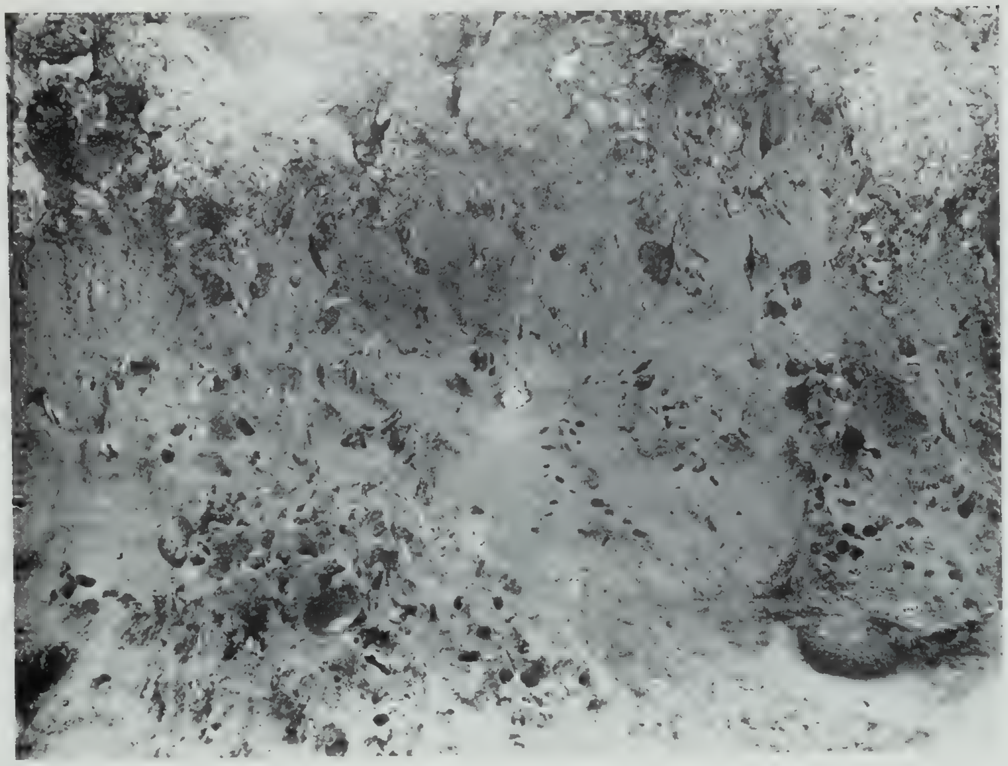

FIG. 1.

FIG. 2.

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DESCRIPTION OF PLATE VI.

FIG. 1.—Near view of a portion of a boulder on the Boulder Tract, showing many old and weathered burrows of *Lithophaga cumingiana* and *L. obesa*, with the shells of dead individuals still *in situ*, pits formed by *Acanthozostera gemmata* and a small specimen of *Tridacna crocea* in its burrow.

FIG. 2.—A portion of the Boulder Tract at Low Isles showing boulders covered with *Ostrea mordax* above and their lower areas much eroded and bored by *Lithophaga*.

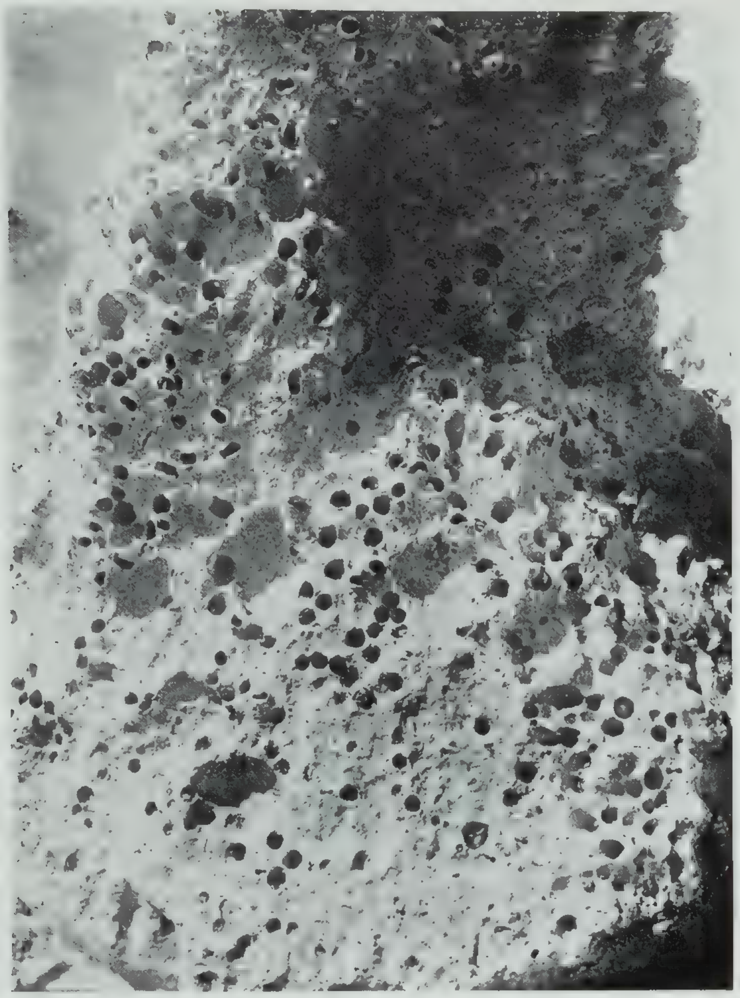

FIG. 1.

FIG. 2.

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